ON THE METHOD OF CELL DIVISION IN TÆNIA.[1]

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Within the last few years the question of the significance of amitosis has pushed its way forward with renewed activity. From the classic views of Ziegler and vom Rath, Flemming and others that amitosis may be expected in unicellular organisms, in degenerating and senescent cells, and in highly specialized and pathological tissues opinion in some quarters has departed widely.

On the one hand the tendency has been to narrow this view. In many of the Protozoa mitosis has been found quite general, at least in some stage of the life cycle, while in certain Rhizopods, as *Arcella* and *Euglypha*, where direct division was formerly thought to be the means of reproduction, it is now known that mitosis is the common method. In the case of highly specialized cells numerous examples are reported in which careful study has shown mitosis as the chief means of division. An example of this tendency is seen in Strasburger's work on the tapetum cells. He found that while the period of mitotic division was very short it was sufficient to account for all the observations that had hitherto been explained on the basis of amitosis. Again the application of improved cytological methods of fixing and staining have thrown into disrepute, to a large extent, the old view of the occurrence of direct division in pathological tissues; indeed the phenomenon of reduction has been described in cancer cells. On these lines of research, then, the tendency has been to limit our notions of the rôle of amitosis in nuclear and cell division.

On the other hand more recently a new line of reasoning has been developed, perhaps more rapidly than the facts warrant. This new line, of which Child is the chief, although not the first exponent, is to the effect that direct nuclear division occurs in rapidly dividing cells and in cases in which an orthodromic or acyclic process is involved. In this connection the statements of

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several writers that mitosis may follow amitosis are to be noted in which they cite cases of direct division in the maturation and pre-maturation stages of various forms. To meet these claims we shall doubtless have to revise somewhat our ideas of the meaning of amitosis, but at present the progress toward such a revision seems to have overstepped the bounds of conservatism.

Among the older workers on this line are Meves, Preusse, and Pfeffer. Meves found amitosis to occur in the early stages of spermatozoön formation in *Salamandra* in the autumn followed by mitosis in the spring, but some of these cells have since been shown to take no part in the formation of spermatozoa. Preusse's work has been much quoted in this connection. He found amitosis in the ovaries of Hemiptera. However, a reinvestigation of this case by Gross in 1901 served to bring it under the theory of Ziegler and vom Rath. Gross showed that this method of cell division did occur but much less widely than described by Preusse. Its occurrence is restricted to two kinds of cells, degenerating and secretory; this, of course, proved that he was dealing with a special case under the old theory. Pfeffer's work on *Spirogyra* has been discredited by Nathansohn; in fact, opinion among botanists is decidedly adverse to the view that amitosis may be followed by mitosis in a single nucleus. This opinion is expressed by Strasburger in his recent summary of the individuality question.

Working on the spermatogenesis of the sparrow in 1900, Loisel saw nuclei which began division by amitosis and later continued by indirect division. He says that the amitosis was not a sign of degeneration; but again, he shows that the greater part of certain spermatocytes and spermatids degenerates. To reach a safe conclusion in this case one must needs know the relation between amitosis in the sex cells and degeneration in the sex products. Degeneration on the part of spermatozoa in the Hemiptera has been traced by Morgan and by Miss Stevens to the absence of a single chromosome. If cells lacking a single chromosome degenerate, certainly one would expect degeneration in cases where part of the sex cells had previously divided by as indifferent a method as amitosis seems to be.

Especial importance has been attached to cases of amitosis in regulatory growth. G. T. Hargitt was the first to suggest this for hydroids. Child's work on *Tubularia* and *Corymorpha* supports this suggestion. In the growth and regulation of *Planaria*, Bardeen and Child have reported amitosis. However, the figures of Bardeen are far from conclusive, and it is very questionable whether they justify the opinion that amitosis is the method of division here. Child has also worked on various other forms among both vertebrates and invertebrates. In several of them his evidence is lacking in some respects. Reference to his work on the cestodes will be made later.

A few workers have described amitosis in the cleavage of the egg and in the early embryonic development of several forms. Hargitt failed to find mitosis of the egg up to the sixteen-cell stage, working on *Clava leptostyla*. Similar results obtain for *Eudendrium* and *Pennaria*. Beckwith, however, has recently shown that his results were due "simply to the fact that the eggs were not obtained at the right time of day. In eggs collected at the proper time (4 to 6 A. M.) there is no difficulty in proving the typical stages of maturation and fertilization." "Maturation and the early cleavages take place by mitosis and not by amitosis." Hickson and Hill have also studied cœlenterate eggs. Hill in his account of *Alcyonium* oögenesis shows that no polar bodies are extruded, no chromosomes are present, the female pronucleus divides irregularly by amitosis and then disappears, and that probably the first cleavage nucleus is formed from the male pronucleus. The evidence is not complete and the case should certainly be reinvestigated. H. L. Osborne described cases of amitosis in the food-ova of *Fasciolaria*. His results have been corrected and enlarged upon by Glaser. The work of Glaser seems to deserve the most careful consideration in regard to this problem ; its bearing on the investigation herewith undertaken is only general, however. Further work on embryos has been done by Child, previously mentioned, and by Patterson on the pigeon's egg. The observations of the latter, while much more extensive than those of Child on the chick embryo, are in agreement with them. Stoeckel thought binucleate ova in man are the result of amitotic divisions. Fick's opinion on the subject of amitosis as expressed in his survey of chromosome hypotheses is based upon the work of Child and Hill and upon his own *a priori* conclusions. He offers nothing new on the problem.

Direct division has been described in other cases of theoretical importance but those mentioned above are perhaps the most significant.

METHODS.

My investigation on the problem of amitosis was suggested by Dr. S. J. Holmes, to whom I owe much for direction during the progress of the work. I have received numerous suggestions from various other workers in the University of Wisconsin, all of which are gratefully acknowledged. My thanks are also due Drs. Grove and Meek, of the Pharmacology and Physiology Departments, for their assistance in collecting material.

Specimens of tape-worms were secured chiefly from dogs. A considerable number of cats was examined, but only one furnished material. The specimens were nearly all fixed in Flemming's fluid, which proved quite satisfactory. Those taken from the cat were fixed in Zenker's fluid to be used with Mallory's connective-tissue stain.

A variety of staining methods was used. Flemming's tricolor stain did not give sufficient sharpness of detail to be of much value. Iron hæmatoxylin is in general satisfactory, but it is to be noted that the nuclei do not differentiate as readily as in many other tissues. The fact that they do not decolorize readily and often do not show their contents clearly must be borne in mind when considering the significance of indentations of the nuclear membrane. Delafield's hæmatoxylin decolorized in acid alcohol gave excellent results. My greatest success, however, in staining this material has been by the use of Kernschwarz with Lichtgrün as a counterstain. Lichtgrün is by far the best stain for cytoplasmic structures that I have tried, its only drawback being the ease with which it fades out.

Two genera and three species of tape-worm have been used: *Tænia marginata* (Batsch), *Tænia serrata* (Goeze), and *Dypilidium caninum* (Leuckart). The last of these is the most favorable for cytological work, but I have only a few specimens of that genus. Even here the nuclei are quite small and not entirely satisfactory owing to technical difficulties. I must protest against the balancing of results obtained from such unfavorable material as that which the cestodes offer against such favorable objects for cytological study as, for example, the Orthoptera. In the cestodes which I have studied, the cells, except the oöcytes, are much smaller than the insect cells, do not stain as readily, and are often obscured by great masses of intercellular material.

Aim.

My aim in this investigation was to obtain definite evidence as to the occurrence of amitosis in cestode tissues. Observations were begun with the hope of bringing into line, in a small measure at least, the account of cell division in this group with the results generally obtained by workers on other forms. Lack of time has prevented the investigation of many of the secondary questions that have arisen. Thus no attempt has been made to give details of chromosome behavior or structure, and the observations have been limited to the method of cell division in the process of oögenesis and in the growth of somatic cells. The discussion, however, includes occasional reference to related questions.

Observations.

Oögenesis. — The female sex cells in the cestodes in question are by far the largest cells in the body. They are in general round with a relatively large nucleus. The cytoplasm is fibrorecticular and to a certain extent granular. Occasionally large dark granules appear, as in Figs. 15, 16 and 17; their nature has not been definitely made out, but they may be yolk nuclei or, perhaps, nothing more than aggregations of smaller cytoplasmic granules. Frequently they serve to obscure the process of mitosis.

No cell organs are located in the cytoplasm of the resting mother cells; but, at some time during the development of the ovarian egg, a mass, probably of yolk, appears there. I have not observed any regularity in the formation of this mass, for some of the early oögonia have it, while it is not present in some oöcytes. The masses, of course, vary in size. Those which are newly formed have a close resemblance with certain stains to a "nebenkern," and, in fact, have been so called. They were first described by Sommer in 1874, and named by him "Nebendotter." This expression, which has the claim of priority, seems unobjectionable except on the score of bringing a foreign word into English; no suitable translation has been suggested, however. On the other hand, the body is not a true "nebenkern," and to call it by that term is a misuse of the word.

Fig. 1 is an early oögonium from *T. serrata*. Here the "Nebendotter" appears as an egg shaped body of even consistency stained darker than the nucleus although lighter than the

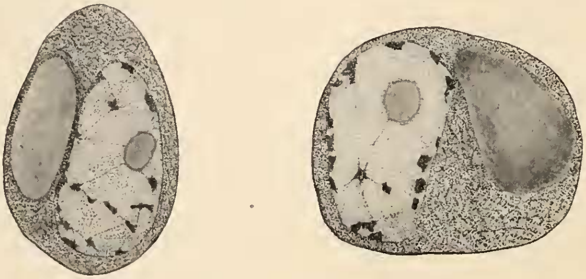

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Fig. 1. Oögonium, stained with iron hæmatoxylin, showing "Nebendotter," and nucleus with chromatin reticulum.

Fig. 2. Oögonium showing same structures as Fig. 1, but from a much later generation.

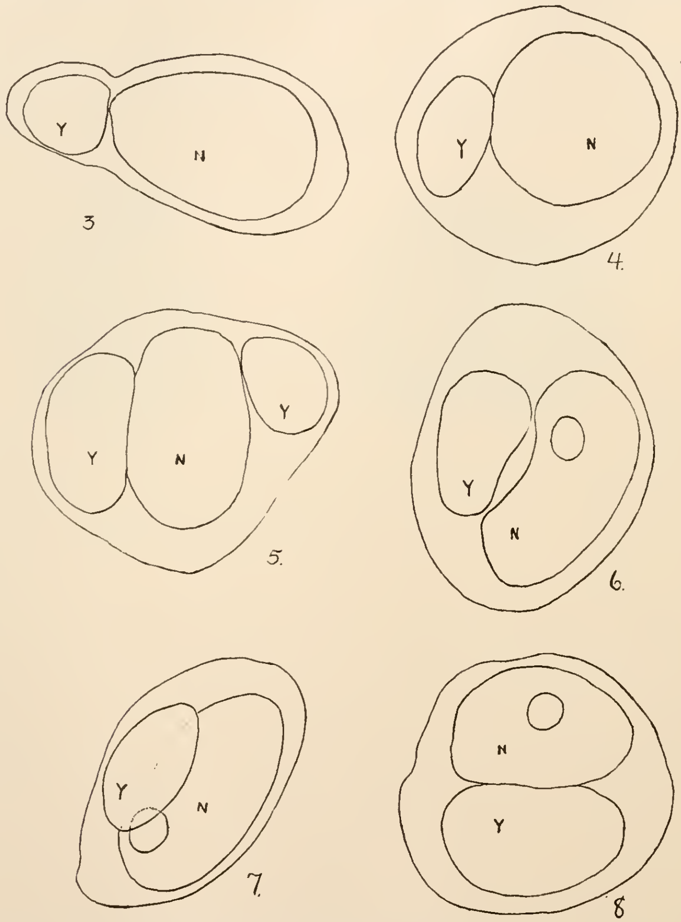
surrounding cytoplasm. Its reactions to various stains deserve metion. With iron hæmatoxylin it stains readily, appearing as a dark homogeneous mass even after a great deal of extraction of the stain. The nucleus and cytoplasm may be entirely decolorized and the "Nebendotter" still show as a dark body, a fact which led to confusion during the early part of my study, as the nucleus was overlooked and the "nebendotter" taken for it. The true state of affairs was not revealed until I had used another method of staining when the appearances which with iron hæmatoxylin had misled me were explained and the structure of the cells became clear. The new reagents were Kernschwarz counterstained with Litchtgrün. Kernschwarz is a weak stain affecting only the nucleus. In my preparations I have seen no trace of it in the cytoplasm or in the "Nebendotter." Lichtgrün stains both nuclear plasm and cytoplasmic structures. The result, then, with this method of staining is as follows: chromatin and nuclear reticulum, blackish; nuclear plasm, very light green; general cytoplasm, dark green, fibro-reticulated; "Nebendotter," homogenous "cheesy" green. This last appearance is very difficult to describe but is recognized very easily.

The "Nebendotter" as such has not been described by Child. One is compelled to suspect that the same appearances which confused me may have misled him. Occasionally a constriction is seen in a "Nebendotter" or there may be two or more distinct yolk masses in a cell. More often, especially in the case of hæmatoxylin slides not well decolorized, the "Nebendotter" does not look unlike a dividing or divided half of the nucleus. Child figures cases in which one half of the nucleus stains darker than the other half. Is this darker half perhaps a "Nebendotter"?

To illustrate the above facts a series of outline drawings is given. They were made with the aid of a Zeiss No. 5 ocular and a Leitz one twelfth objective (oil immersion). In each case *n* represents the nucleus and *y* the "Nebendotter." In studying these figures one can easily see how refractive properties may have obscured the boundaries between the various parts. All figures in this series are of resting cells such as are shown in Figs. 1 and 2. Figs. 3 and 4 resemble cases of unequal constriction of the nucleus, Fig. 8, of equal constriction, and Fig. 5 a nucleus divided into three parts by amitosis. Fig. 6 suggests that division began at the center and progressed outward. Compare these figures with those from Child's paper on oögenesis (6): Fig. 1 with his Fig. 29; Fig. 2 with his Fig. 9, *b*; Fig. 3 with his Fig. 8, *b*; Fig. 6 with his Fig. 11, *A*, *a*; Fig. 7 with his Fig. 13, *A*; and Fig. 8 with his Fig. 10, *A*. The similarity is very suggestive.

Resting nuclei are seen in Figs. 1, 2, and 9. Fig. 9 is lacking in a "Nebendotter." The nuclear plasm in the resting condition seems homogeneous throughout and takes a very light stain. The nuclear membrane is a very delicate structure, showing as a thin line in some cases, while in others its location is marked only by the inner edge of the cytoplasmic reticulum. A nucleolus is usually present in the early stages of cell formation; it takes a very light stain in some cases resembling the "Nebendotter." I have never seen a divided or dividing nucleolus.

With regard to their chromatin content the nuclei of *Tænia* differ from those of *Monieza*. Child states that "the only deeply staining portions of the nucleus up to this time (end of oögonial division period) have been the nucleolus and frequently a few other granules." In another place he says that the nuclei do



FIGS. 3–8. Outline drawings from oögonia showing various relations assumed by the nebendotter and nucleus. *N*, nucleus; *Y*, "Nebendotter."

not contain any definite reticulum. That his statements do not hold for *T. serrata* may be seen from my Figs. 1, 2 and 9. The chromatin content is small in amount, but it can be seen in definite masses which are scattered over the periphery of the nucleus and which are connected by definite strands of linin. The reticular character of the chromatin and linin is clearly shown with Kernschwarz and Lichtgrün. This description answers not only for late oögonia but also for the early ones and for the oöcytes. Fig. 9 is an early oögonium.

Fig. 10 illustrates the early condition of the spirem stage. Oögonia in this stage and slightly later are very numerous in certain lots of material. In other lots I find many resting stages. Anaphases and telophases, too, are not difficult to find but metaphases are conspicuously absent. This probably means that the metaphases are of short duration. It also indicates a fact which I believe to be very pertinent to the question of the frequency of mitoses; namely, a periodicity[1] with regard to

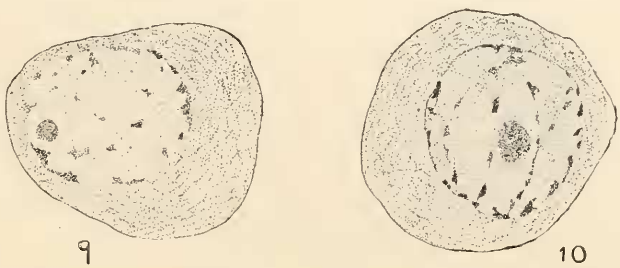


FIG. 9. Resting oögonium with a definite chromatin reticulum; no "Nebendotter" present.

FIG. 10. Oögonium; very early prophase, spireme formation beginning.

FIGS. 9–17. From cells stained with Kernschwarz and Lichtgrün.

the divisions. It is well known that physiological factors may govern the time of mitotic divisions. A case in point is that recently described by Beckwith, previously mentioned; likewise, in certain insects and in many plants mitosis occurs at night only. The fact that many nuclei from one lot are in the same stage of division indicates, I believe, the effect of some physiological factor. What that factor is, I can only conjecture. Perhaps mitotic periods may occur only after a more or less prolonged fast on the part of the host, for then the energies of the parasite are not directed towards the assimilation of food.

During the maturation period the regular course is followed.

[1] This expression is not intended to imply that a definite amount of time intervenes between successive periods; they may recur at irregular intervals depending on some physiological factor.

Figs. 13 to 17 illustrate the process, but no attempt is made to give even a meagre outline of the behavior of the chromosomes in this period. However, attention is called to the appearance of the spindle. While spindle formation is quite regular, the achromatic fibres do not stain well and frequently the entire structure is overlooked. This fact taken with the smallness of the chromosomes and the prominence of the large cytoplasmic granules may well serve to veil the process of mitosis. In many cases one does not, at first, distinguish between the chromosomes and the


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FIG. 11. Oögonium; polar view of an anaphase. This figure and the next are from early generations of oögonia.

FIG. 12. Oögonium; polar view of a telophase.

cytoplasmic granules, so nearly alike may they appear. While Fig. 15 shows clearly its mitotic character, the cell from which it was drawn was overlooked for a long time.

Fig. 17 is a case which suggests an "endogenous" division. According to Child, an endogenous division is that of a nucleus into two nuclei within the old nuclear membrane. Upon a superficial inspection the cell in question seemed to be in process of such division as shown by the outline in Fig. 18. Careful study, however, revealed the mitotic nature of the division. It is a late telophase with the chromosomes disintegrating; remnants of asters may be seen, as can a Zwischenkörper.

The appearance of this cell suggests the question of the relation between nuclear and cell division. Botanists have recognized the distinction between the two processes much more generally than have zoölogists. The latter have been accustomed to regard nuclear division as a sign of immediate cell division. Very often this is not the true state of affairs, for nuclear division may never be followed by cell division (Marshall), or a considerable period of time may elapse before a cell plate is formed. Fig. 17 shows no sign of cell division although mitosis is almost complete. This is not an infrequent occurrence; actual nuclear division and certainly cell division may lag well behind spindle and chromosome division. Herein lies a fruitful cause for misinterpretation. A nucleus in which chromosome division has been completed would give every appearance of direct division upon constriction and subsequent division. Two nuclei in a single cell which had not begun to form a cell plate would also be misleading.

No true case of amitosis has been observed in the egg cell formation of the *Tænias* upon which I have worked.

Somatic Tissues. — The somatic tissues of tape-worms inside the cuticle include muscle fibres, excretory and genital organs, and a primitive nervous system. Surrounding all of these organs and filling all interstices is a large mass of parenchyma. A detailed study of all of these structures has been made by Child for *Monieza.* He reports that many cases of amitotic division occur and that illustrations of this fact might be multipled indefinitely.

I have made no investigation of the method of cell division in the excretory or nervous systems of *Tænia.* There is no reason

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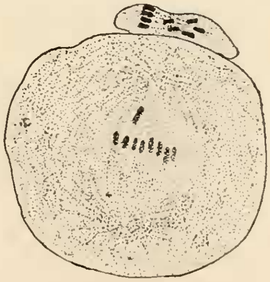

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FIG. 13. First oöcyte; late metaphase.

FIG. 14. Second oöcyte; equatorial plate stage, first polar body dividing.

to believe, however, that the method of division in those organs differs from that of the genitalia or of the muscle fibers. We have in all of these systems cells that are specialized to a high degree. Even if amitosis be found here where rapid growth may be taking place that fact loses significance when the degree of specialization is considered. The various cell generations of a differentiating tissue differ from earlier generations only in a gain in specialization and a loss in reproductive potentiality. Rapidity of division in these cases is a negligible factor. We are simply dealing with a special case under the old theory, if amitosis be found to obtain here. Amitosis, then, may well be expected in these systems.

The facts observed in the genitalia of *Tænia* do not bear out fully that expectation. The structure of the genital ducts and organs can be made out clearly and nuclei, cytoplasm, and intercellular substance seen. Yet cases of amitosis have not been demonstrated. On the other hand, a mitotically dividing nucleus is found only rarely. This may mean that mitosis is of very

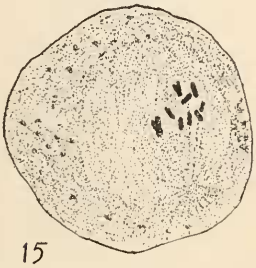

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FIG. 15. Second oöcyte; early anaphase, spindle stained very lightly. Figs. 15–17 show the large cytoplasmic granules.

FIG. 16. Second oöcyte; telophase.

short duration, or more probably, that it is of short duration and occurs in waves; or, again, it may indicate that the nuclei divide amitotically. But whichever interpetation we may accept we do no violence to the theory of Ziegler and vom Rath.

The muscle-cells also furnish only negative evidence of amitosis. They are large, spindle-shaped cells from which contractile fibers extend. The cytoplasm is densely reticulated, rarely exhibiting the vacuolated structure described by Child (8). The quantitative relations of cells and fibers at different periods of development are of interest. Relatively more muscle cells are present in a young proglottid than in an old one, but the muscle fibers are much more developed in the later stages. The significance of this relation, which agrees closely with a similar parenchymal relation, will be discussed later. While satisfactory evidence as to the usual method of cell division has not been obtained, the observations on the material at hand favor mitosis as typical.

The meaning of amitosis in the parenchyma is of quite different import from that in specialized tissues. Parenchyma is a tissue from which others are derived; it is neither highly specialized, degenerating or pathological. The occurrence of amitosis here, therefore, would not be in line with the old theory.

Concerning the nature of parenchyma there has been much

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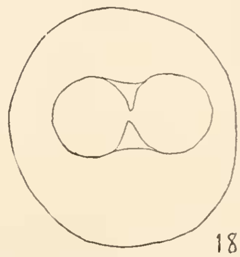

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FIG. 17. Second oöcyte in which mitosis is nearly complete, yet no sign of cell division. The daughter nuclei are being constricted apart and the chromatin masses are disintegrating. Zwischenkörper present.

FIG. 18. Outline drawing of Fig. 17. It gives the appearance of an "endogenous" division by amitosis. Fig. 17 shows that appearance to be entirely superficial.

controversy, but it is beyond the scope of this paper to enter into a discussion of the question or of the literature regarding it. In connection with an account of the method of cell division, however, a few observations concerning it cannot be avoided. The older view held by Leuckart and his followers was that the parenchyma develops from rounded and polyhedral cells, the latter sending out processes which interlace about the former. Moniez and his followers offered an opposed view. Opinion has by no means become settled even now. Child speaks "of the parenchyma cells if the syncytium which composes the parenchyma can properly be said to be composed of cells."

Parenchyma consists of calcareous bodies and irregularly shaped cells lying in a mass of material which seems to be intercellular. Of these, the first do not enter into the question under consideration, and the intercellular matter only figures as a ground substance in which the cells are imbedded. The cells vary in shape from elliptical and spindle-shaped to an irregular form with many protoplasmic processes. In size there is also much variation, due, largely, to the variation in the amount of the cytoplasm, for the nuclei do not exhibit any such striking quantitative differences as does the cytoplasm. The cells do not seem to form a syncytium of which the ground substance is a part, as some writers have stated. The evidence seems to me to indicate that the ground substance bears a relation to the parenchyma cells similar to that borne by the intercellular matter of connective tissue, for example, to the connective-tissue corpuscle. That the parenchyma cells have definite boundaries is brought out clearly in the Lichtgrün preparations. I have seen no evidence for thinking the ground substance continuous with the cytoplasm. The nuclei of the cells show uniformity of structure as well as of size; they have a chromatin reticulum and usually a nucleolus. The parenchymal cell is thus seen to be a definite structure with a typical nucleus and a varying amount of cytoplasm.

Fig. 19 is a resting parenchyma cell of characteristic appearance. The cytoplasm is drawn out into strands upon the number

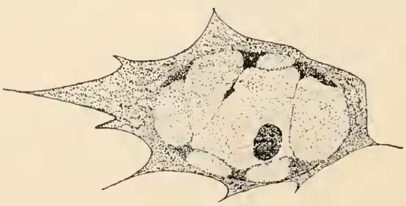

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FIG. 19. A typical parenchyma cell in the resting condition. This cell is from a proglottid in which the sex organs are only partially developed.

and size of which depends the width of the cytoplasmic band about the nucleus. Parenchyma shows regional differentiation in the relative amount of ground substance and cells and in the modification of the cytoplasmic parts of the cells only. In the younger cells the cytoplasmic strands are less numerous and frequently extend only a short distance. In older regions more cytoplasm is drawn out into the strands, leaving but a thin layer about the nucleus.

Professor Child has assumed through all his work that the absence of mitotic figures in tissues known to be growing rapidly is evidence of the occurrence of division by amitosis. This assumption is, of course, based on good *a priori* reasoning, but I do not believe that it is borne out entirely by the facts. In *Tænia* the parenchymal cells are relatively less in number in the old tissue than in the younger, a relation which is only partially explained by the fact that other kinds of cells develop from the parenchyma. On the other hand, the ground substance in the young proglottid is more spongy and less in amount than in the older portions of the animal. These observations show that the growth of the parenchyma is not due alone to cell multiplication but also to the formation of new intercellular matter and to the greater development of the cytoplasmic strands. The growth of the cestode soma is due chiefly to the growth of the parenchyma and of the muscle cells and fibers. Other tissues, except the sex products, are practically negligible in accounting for increase in size. With regard to the growth of the muscle fibers a similar condition obtains in them as in the parenchyma, as is shown above. Thus we find growth depending not so much on the increase in the number of cells as in the increase in amount of products of cellular activity, that is, in fibers and intercellular material. Therefore, the rapidity of growth in the cestode body does not necessarily postulate a large number of dividing cells.

As to the method of cell division little can be said. No traces of amitosis appear. Cases of several nuclear divisions in a common cytoplasmic mass such as are figured by Child (11) for *Monieza* are not to be seen in *Tænia*, nor is any explanation of them afforded by the latter genus. I have also observed no cases of mitosis. The evidence at hand, I believe, does not warrant any conclusion as to the method of cell division in the parenchyma of this form.

Summary.

1. Amitosis has not been found to occur in the oögenesis of the cestodes studied.

2. All observations on the process of oögenesis point to mitosis as the usual method of cell division.

3. The presence of a "Nebendotter" which has peculiar staining properties gives a misleading appearance of amitosis.

4. Maturation is of the typical form.

5. Indirect evidence strongly suggests that physiological factors influence the frequency of mitotic divisions.

6. Nuclear divisions are not always followed immediately by cell division.

7. Only negative evidence as to the method of division in somatic structures has been found; there is no satisfactory evidence of amitosis and mitosis is not abundant.

8. Rapidity of growth in the somatic tissues of the cestodes body does not necessarily postulate many division figures.

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[1] Endeavor has been made to include in this list the more important papers referring to the recent trend of opinion as to amitosis, although some have no direct bearing on the case of *Tænia*. In numbers 1 and 21 it has been impossible to give exact references.

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